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Population dynamics of *Cognettia sphagnetorum* (Enchytraeidae) in a Scots pine forest soil in Central Sweden

Helène Lundkvist

With 9 figures

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1. Introduction

Enchytraeids are known to be abundant in coniferous mor humus soils. *Cognettia sphagnetorum* (Vejd.) is the predominating species and often contributes 90—100% of the enchytraeids (Nielsen 1955a, O'Connor 1957, Nurminen 1967, Abrahamsen 1971). Thus, *C. sphagnetorum* might have a considerable impact on soil processes, such as nutrient turnover and carbon flux.

In general, soil animals are considered to play a vital role in litter decomposition as they increase the substrate area available to microorganisms by fragmentation of litter and through defaecation of partly digested litter particles. Also, by their consumption of microbial cells, cellularly bound nitrogen may be decomposed into less complex compounds that become available following excretion to plants either directly or after the action of nitrifying bacteria. Furthermore, rather large pools of animal-bound nutrients may be released or retained at intervals due to animal population and biomass cycles.

As pilot studies revealed that *C. sphagnetorum* made up the largest specific fraction of animal biomass in the forest site investigated (0.5—3 g m^{-2}) (Axelsson et al. 1974) it was expected to have a particularly great impact on the system.

C. sphagnetorum is unusual in its mode of reproduction as it reproduces asexually through fragmentation. The species may reach a lenght of about 65 segments and upon fragmentation divides into two or more pieces which must be at least four to six segments long in order to regenerate a new head and/or tail (Christensen 1959, Standen 1973).

The present investigation arose from the questions: What is the impact of *C. sphagnetorum* on decomposition processes and nutrient turnover and carbon flux in the soil? Why does it dominate among the enchytraeids in coniferous forests? Why does it fragment for reproduction?

In order to approach the answers to these questions a series of monthly samplings were undertaken for estimations of abundance, biomass, respiration and nitrogen content of *C. sphagnetorum* during a one-year cycle and an additional growing season. The lack of discrete generations in *C. sphagnetorum* complicates estimation of population turnover as well as respiration and elemental turnover etc. The enchytraeids sampled therefore had to be individually measured (cf. below) to provide the basis for such calculations. Population data presented below will also be used in preparing a population model for *C. sphagnetorum* at a coniferous forest site (Lundkvist, in prep.).

The investigation was carried out within the Swedish Coniferous Forest Project. Parallel studies in place and time were performed on soil bacteria (Clarholm & Rosswall 1980) soil fungi (Söderström & Bååth 1978) nematodes, tardigrades and rotifers (Sohlenius 1977, 1979) and micro- and macroarthropods (Persson, in prep.). A synthesis of these coordinated studies as regards trophic structure and carbon flow through the soil organisms has been given by Persson et al. (1980).

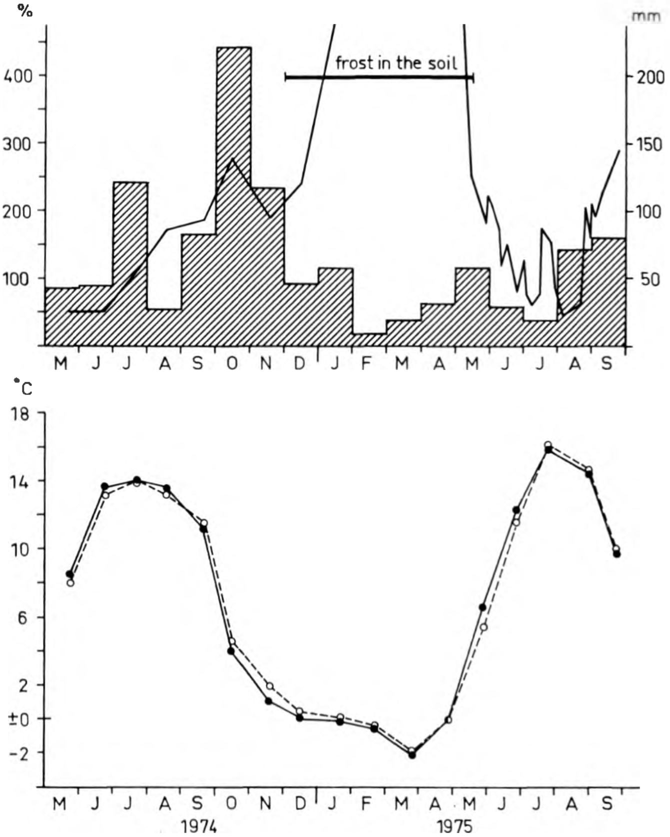

Fig. 1. Above: Monthly precipitation (hatched columns), soil moisture in the humus layer and duration of frost in the soil (horizontal bar) during the investigation period at Ih V, Jädraås. Below: Soil temperature in the 120-year-old Scots pine stand Ih V, Jädraås in the humus layer (●) and in the mineral soil (○) about 10 cm beneath the litter layer.

2. Site description

The research site, described in detail by Axelsson & Bråkenhielm (1980) is an 120-year-old Scots pine (*Pinus sylvestris*, L.) stand on glacifluvial sand at Ivantjärnsheden (Ih V) in Jädraås, Central Sweden (60°49′ N, 16°30′ E; 185 m above M.S.L.). The long-term mean annual air temperature is 3.8 °C. The warmest month is July, +15.8 °C, and the coldest is January, −7 °C. The long-term mean annual precipitation is about 600 mm. According to Axelsson & Bråkenhielm (1980) the vegetation belongs to the association Cladonio-Brometum (boreale) K—L 1967 (Kielland-Lund 1973) or to the lichen and lichen-dwarf-shrub forest types (Ebeling 1978). The soil type is an iron podsol. The organic layer in a core sample was 2.6 ± 0.3 cm (Sohlenius 1979).

Soil temperature at 2 and 5 cm depths was measured with a Grant recorder during the research period, with the exception of June—August 1974 when temperature data from a nearby younger pine stand were used. Compilation of temperature data into monthly means (Fig. 1) was done by T. Persson & B. Vegerfors-Persson (unpublished). The soil water content of the different soil horizons (Fig. 1) was gravimetrically determined, after drying at 105 °C (Jansson 1977, Clarholm 1977, Bååth & Söderström, pers. comm.).

3. Methods

3.1. Sampling design and sample treatment

The research area, 100 × 200 m was divided into 10 × 10 m plots 18 of which were randomly chosen for enchytraeid sampling. The same 18 plots were used during the whole investigation period but the sampling position was moved about 2 m each time. Samples for studies of other soil fauna groups and microorganisms (cf. above) were taken in the close vicinity of the enchytraeid samples.

Soil samples for the enchytraeid extractions were taken with a soil corer and measured 22.2 cm^2 × 20 cm (34.2 cm^2 × 20 cm in February when a larger corer was used because of hard frost). The cores were divided in the field into three soil horizons; the organic horizon, including living mosses and lichens (litter and humus) (A_{00} – A_{02}), the eluvial (bleached) (A_2) and the illuvial (enrichment) (B). The enchytraeids were extracted from the soil with a modified Baermann technique (O'Connor 1962). They were counted alive and determined to species according to Nielsen & Christensen (1959).

The investigation covered the period from May 1974 to September 1975 with monthly samplings around the 20th of each month with the exception of March 1975 when the sampling was omitted because of very deep and hard frost.

3.2. Size classification of worms

The specimens of *C. sphagnetorum* were classified to size according to their number of segments. Notes were also made whether the measured specimen was a complete worm or a head-, middle- or tail fragment. The size classifications were made either on the living enchytraeids or, on most sampling occasions, on enchytraeids preserved in 50% ethanol and then transferred to glycerine preparations. Size measurements were not undertaken on specimens that were judget to have been fragmented during extraction, or on those that had suffered from extraction and started to macerate. On average, 67% (s.e. = ± 3.7) of the enchytraeids sampled were measured on each sampling occasion.

The size structures of the enchytraeid population in different months were compared through analysis of variance. For this purpose the mean worm sizes in each soil horizon and in the whole soil core were calculated for all sampling points (n = 18). These mean values were then used in a series of one-way analyses of variance, whereby between month, between sample as well as between worm variances were calculated.

The measured worms at each sampling point were also the basis for estimations of the mean fresh weight, dry weight, respiration and nitrogen content per worm and month, as presented below.

The population biomass, respiration and nitrogen content on each sampling occasion were estimated from abundance data (y) and mean worm data (x) to get the product $z = x \cdot y$ for each sampling plot (n = 18). Thus $\bar{x}$, s^2 and s.e. could be calculated for each sampling occasion to give the monthly estimate of the different population characteristics per m^2.

3.3. Biomass estimates

Dry weight biomass and fresh weight biomass were determined on individual worms of different sizes by weighing them on a microbalance (Cahn Electrobalance Model 4700).

Dry weight measurements were performed on worms that were freeze-dried for 5 days. This procedure was found to dry out worms as efficiently as 24 hrs. at 85 °C. However, freeze-dried worms were easier to handle.

The equation $y = ax^b$ was fitted to data, where y is weight (μg) and x is number of segments. This dave the equations

$y_s = 0.016\, x^{2.136}$ (r = 0.88)

for worms without gut contents, i.e., starved 4–5 days in water at 6 °C before drying and

$y_{ns} = 0.217\, x^{1.509}$ (r = 0.84)

for worms not starved.

To yield the dry weight of the gut contents these two equations were compared stepwise in the range x = 15 to 55 segments and with an interval of 1 segment. According to this calculation the mean gut content was 12.27 μg (s.e. = 0.53).

Determinations of fresh weights were made by weighing the worms in a drop of silicone fluid (Lundkvist 1978). These weighings had to be done on worms with gut contents. However, corrections for gut contents were made for each weighed worm from the calculated dry weights of gut contents (cf. above) by assuming that the water content in the fresh gut content was 200% of the dry weight. This is a reasonable figure compared to the humus substrate where the worms lived.

The equation above $y = ax^b$, was fitted to the corrected fresh weight data resulting in

$y_f = 0.019\, x^{2.6379}$ (r = 0.91)

A stepwise comparison of the fresh weight and dry weight equations showed that the dry weight averages 14.86% (s.e. = 0.46) of the fresh weight.

The weight structures of the enchytraeid population for different months were compared in analogy with the size structure, i.e., the mean weight per worm and sampling point were calculated and used in an analysis of variance.

3.4. Respiration estimates

The respiration rates of individual specimens of *C. sphagnetorum* were calculated from the regression equation given by Persson & Lohm (1977);

$Q = 33.6 \cdot w^{0.67}$

where Q denotes respiration at +20 °C ($mm^3\ O_2\ h^{-1}$) and w denotes live body weight (g).

The respiratory rates at field temperatures were calculated after correction with a temperature coefficient obtained from a model based on hourly field temperature measurements at 2—5 cm and 5—10 cm soil depth for the A_{00}—A_{02} and A_2 — B horizons, respectively, and the assumption that $Q_{10} = 2$ for temperatures over + 5°C and is linearly increasing for temperatures from —5 °C to +5 °C (PERSSON et al. 1980).

Assuming an RQ of 0.8 the estimated respiration data are expressed as g carbon respired per worm and month. Monthly population respirations were compared in analogy with size and biomass comparisons.

3.5. Nitrogen content

The nitrogen contents and the C/N ratio of *C. sphagnetorum* were determined on worms collected in October 1978 at Jädraås. The worms had been allowed to empty most of their guts during one night's storage at +5 °C. The element determinations were made on a Carlo-Erba Elemental Analyzer 1106 at the Department of Chemistry, Swedish University of Agricultural Science, Uppsala.

4. Results

4.1. Abundance

During the whole sampling period *C. sphagnetorum* dominated completely over other enchytraeid species. Totally, over the 16 samplings only four specimens of other species were found; viz. 1 *Mesenchytraeus pelicensis* (LEVINSEN) and 3 *Mesenchytraeus* spp. The abundance of *C. sphagnetorum* during the investigation period is given in Fig. 2. The density, no. m^{-2} was at its lowest, below 10,000 ind m^{-2}, in spring and early summer, increasing to about 23,000 ind m^{-2}, in the middle of the summer and decreasing in early autumn. In late autumn and winter the population built up its numbers to around 23,000 ind m^{-2} before the spring decline.

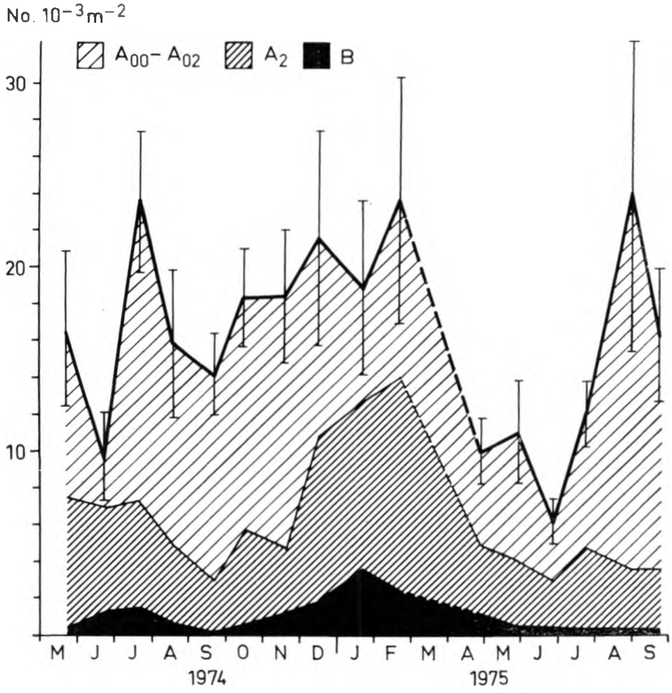

Fig. 2. Abundance (no. m^{-2}) of *Cognettia sphagnetorum* at Ih V, Jädraås. Mean values and standarde errors are given for the total soil depth sampled, whereas mean values only are given for the different soil horizons. Significant differences are given in the appendix (matrix 1).

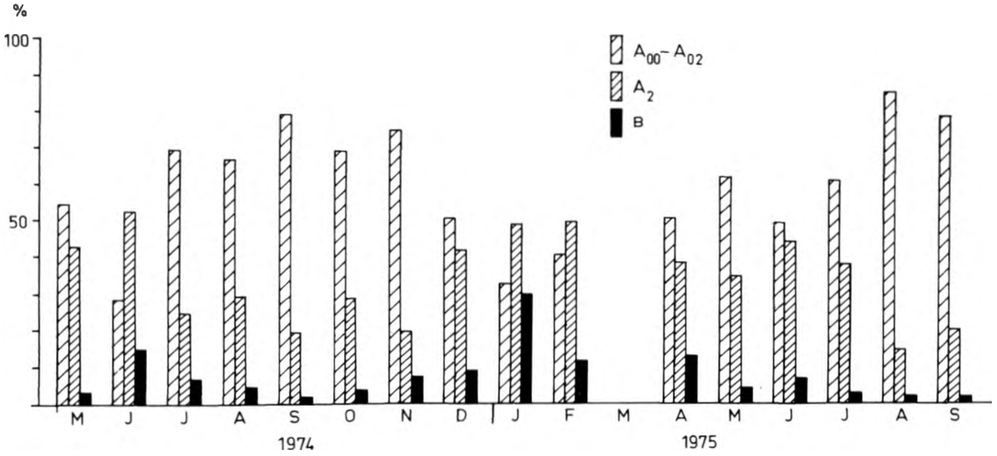

Fig. 3. Vertical distribution of *Cognettia sphagnetorum* given as the percentage of the population found in different soil horizons on each sampling occasion at Ih V, Jädraås.

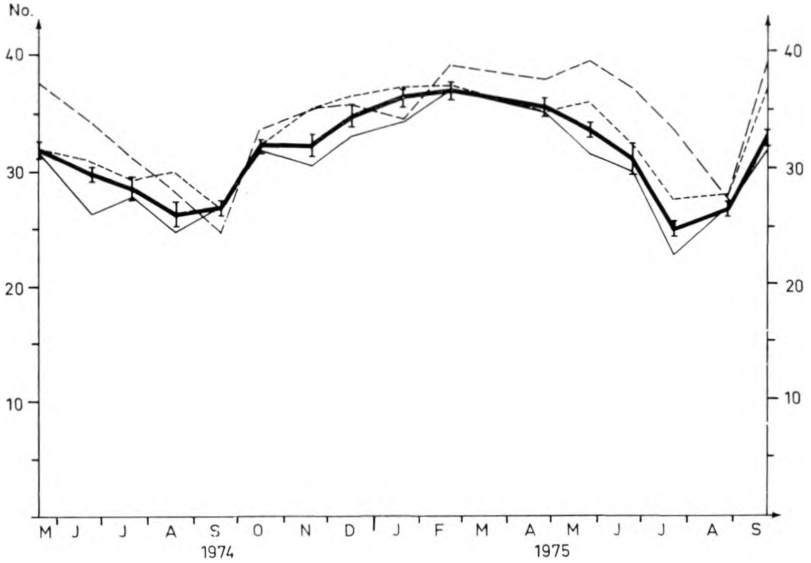

Fig. 4. Size distribution (no. of segments) of *Cognettia sphagnetorum* in different soil horizons at Ih V, Jädraås, during the investigation period. Mean values and standard errors are given for the total soil depth sampled (▬▬) whereas mean values only are given for the different soil horizons: A_{00}—A_{02} (— — —), A_2 (-------) and B (———). Significant differences are given in the appendix (matrix 2).

4.2. Vertical distribution

The vertical distribution of *C. sphagnetorum* showed seasonal variations (Fig. 3). In summer and early autumn $^2/_3$ or more of the population was generally found in the A_{00}—A_{02} horizon but in January and February only $^1/_3$ was found in these layers. One remarkable exception from the general tendency was in June 1974 when 70 % of the enchytraeid population was found in the mineral soil.

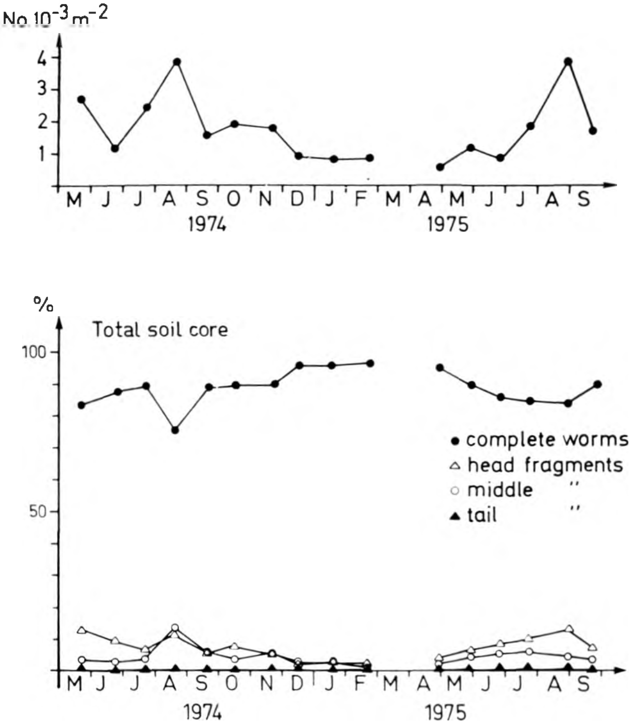

Fig. 5. Above: The total abundance of *Cognettia sphagnetorum* fragments at Ih V, Jädraås. Below: Relative distribution of complete worms and fragments in the total soil depth sampled.

4.3. Size distribution

The size distributions over the year and in the different soil horizons are given in Fig. 4. There was a decrease in mean worm size with minima in late summer or early autumn in both 1974 and 1975. Between these points there was a rather long period during the winter larger worms. The total number of fragments (Fig. 5) as well as the relative proportion of fragments (Fig. 5) peaked in late summer and early autumn, respectively, in the two years. The worms thus seemed to increase in fragmentation rate in summer, although fragmentation to some extent occurred throughout the year. The amplitude in mean worm size for all soil horizons considered together was 12 segments, from 24 to 36 segments.

The range in sizes of whole worms, head, middle and tail fragments over the investigated period and in different soil horizons is shown in Table 1.

A comparison of worm size in different soil horizons reveals that mostly large worms were found in deep layers (cf. Fig. 4). The average worm was generally about 4 segments larger in the B horizon than in the A_{00}—A_{02} horizon. The size in the A_2 horizon was intermediate.

Table 1. Minimum and maximum size (no. of segments) of *Cognettia sphagnetorum*, whole worms and fragments, found at Ih V, Jädraås from May 1974 to September 1975

Soil horizon	head min.—max	middle min.—max.	tail min.—max.	whole min.—max.
A_{00}—A_{02}	6—39	7—16	7—49	12—62
A_2	10—41	8—29	8—34	10—60
B	12—30	not found	17—24	14—56
Total	6—41	7—29	7—49	10—62

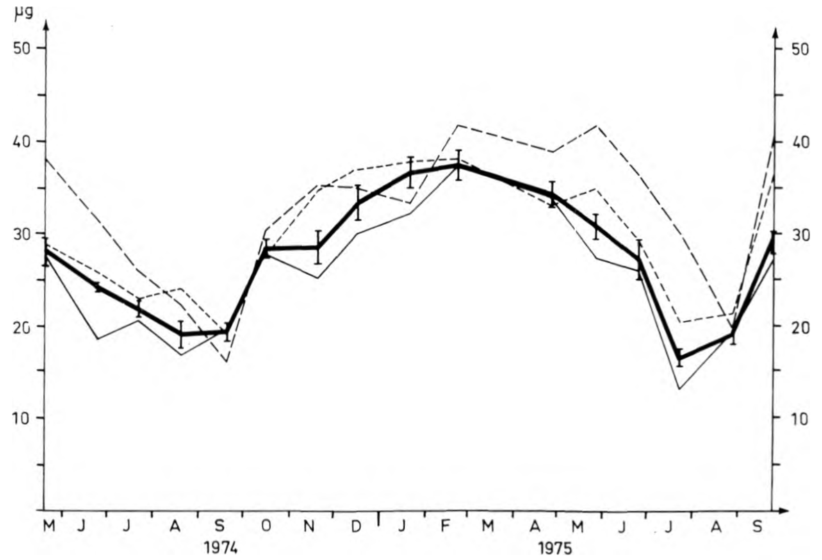

Fig. 6. Average dry weight of individual *Cognettia sphagnetorum* at Ih V, Jädraås (cf. Fig. 4., for symbols). Significant differences are given in the appendix (matrix 4).

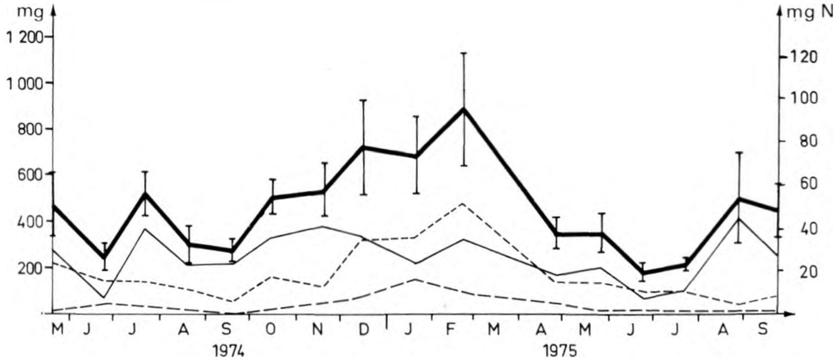

Fig. 7. Average dry weight (left y-axes) and nitrogen content (right y-axes) of the population of *Cognettia sphagnetorum* at Ih V, Jädraås (cf. Fig. 4. for symbols). Significant differences are given in the appendix (matrix 6).

4.4. Biomass

The mean dry weight of the worms, on average comprising 14.9 % of the fresh weight, of the worms is given in Fig. 6. The weights showed essentially the same variation over the year and soil horizons as did size. However, the shapes of the curves differed in a way that would be expected from the exponential relationship between worm size (no. of segments) and worm weight.

The population biomass, i.e. (abundance multiplied by individual biomass) peaked at the same time as the abundance, viz. in early summer 1974, winter 1974/75 and in summer 1975. Fig. 7 shows the dry weight biomass of the population. The population fresh weight biomass gives a very similar graph although the absolute values on the y-axes are 6.7 times higher (data not shown). Contrary to the abundance curve, the winter peak of the population biomass curve exceeded the summer peaks. This is a reflection of the larger worm size during the winter (cf. Fig. 4). The vertical distribution of the enchytraeid biomass followed that of the abundance with two excepts, June and July 1975. On these occasions there was a higher worm biomass in the A_2 horizon than in the A_{00}—A_{02} horizon despite the opposite condition as regards abundance.

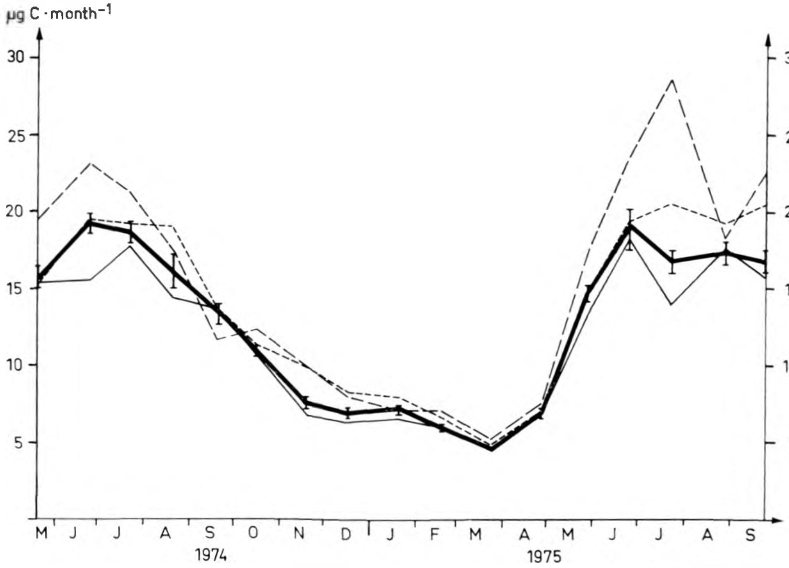

Fig. 8. Average respiration of individual *Cognettia sphagnetorum* at Ih V, Jädraås (cf. Fig. 4. for symbols). Significant differences are given in the appendix (matrix 7).

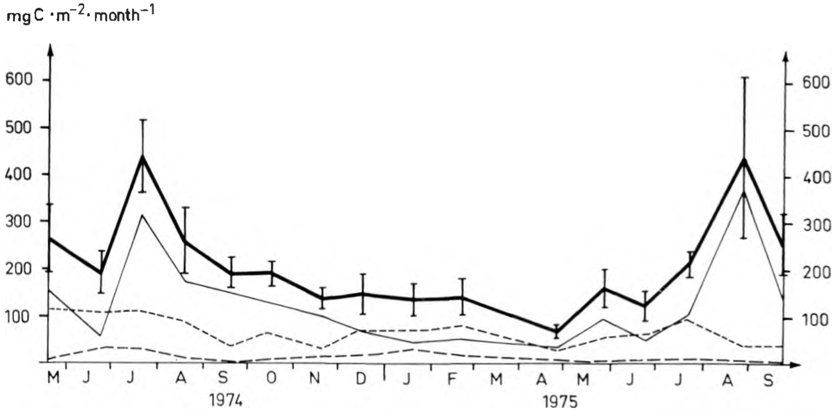

Fig. 9. Average respiration of the population of *Cognettia sphagnetorum* at Ih V, Jädraås (cf. Fig. 4. for symbols). Significant differences are given in the appendix (matrix 8).

4.5. Respiration

The fluctuations in worm mean respiration over the year (Fig. 8) roughly followed the soil temperature curve (Fig. 1). Individual respiration values reached their highest levels, c. 20 μg C month^{-1}, during the summer and declined in winter to c. 6 μg C month^{-1}.

Differences in worm respiration between the soil horizons followed the difference in the worm weight. Thus the worms in the mineral soil layers respired more than those in the organic soil.

Population respiration (Fig. 9) showed maxima in July 1974 and August 1975 when the population of *C. sphagnetorum* respired 440 mg C m^{-2} month^{-1}. The lowest population respiration, 68 mg C m^{-2} month^{-1}, occurred in April 1975.

The vertical distribution of the population respiration diverged from the vertical distribution of population abundance only in June 1975 when the respiration in the A_2 horizon exceeded that in the A_{00}—A_{02} horizon. The total amount of carbon respired over the year from May 1974 to April 1975 was 2.2 g C m^{-2}. The total carbon respiration during May to September 1974 was 1.3 g C m^{-2}, whereas during the same period in 1975 it was 1.2 g C m^{-2}.

4.6. Nitrogen content

The nitrogen content of *C. sphagnetorum* from the Jädraås site was 10.8 % of the worm dry weight. The C/N ratio was 4.71.

From the generalization that the nitrogen content of *C. sphagnetorum* is constantly 10.8 % of the dry weight, it follows that the fluctuations in nitrogen bound by worms during the research period paralleled the dry weight curve of the population. Thus, from September 1974 to February 1975 65 mg N m^{-2} was retained by the enchytraeid population, which at most contained 95 mg N m^{-2}. From February to June 1975, 76 mg N m^{-2} was released by the population and the minimum amount of nitrogen bound in the worms was 19 mg N m^{-2}.

5. Discussion

5.1. Species composition

The species composition of Enchytraeidae at the Jädraås site, i.e., more than 99 % dominance of *C. sphagnetorum*, appears to be typical of a poor pine forest of mature age. In comparisons of the enchytraeid fauna at different coniferous forest sites, ABRAHAMSEN (1972) in Norway, and NURMINEN (1967) in Finland, found that *C. sphagnetorum* made up 96—99 % and 98—100 %, respectively, of the enchytraeid population in pine forests at about the same latitude as the present site. The biological reason for the dominance of *C. sphagnetorum* over other enchytraeid species might be found in its faculty of asexual reproduction. STANDEN (1973) suggested that asexual reproduction is an adaptation to conserve energy and nutrients in a poor environment. An additional hypotheses could be suggested from the general trends that have been outlined for asexual reproduction by, e.d., GHISELIN (1974) and GLESENER & TILMAN (1978). They correlate asexuality with highly predictable habitats although they differently emphasize the predictability of the abiotic and biotic conditions.

In a coniferous forest soil, like the one I have examined, dry periods occur with fairly high regularity, and moisture levels decrease below 50 % of soil dry weight (cf. Fig. 1) at least in some microsites. The enchytraeids are sensitive to this desiccation. Thus, *C. sphagnetorum* does not survive a higher soil *p*F than 4 (NIELSEN 1955b, ABRAHAMSEN 1971). In a raw humus this is roughly comparable with a soil moisture content of c. 50 % water of soil dry weight (ABRAHAMSEN 1971).

Unter these dry conditions it is likely that the enchytraeids survive only in restricted favourable microsites. Reproduction by fragmentation may be profitable for the worm in the quick recolonisation of its habitat when moisture improves. Thus, in habitats where events of severe drought occur regularly, enchytraeid species with asexual reproduction may be favoured.

5.2. Vertical distribution

The general tendency in the vertical distribution of *C. sphagnetorum* with the highest proportion of worms generally found in the organic soil layers, agrees well with earlier findings on Enchytraeidae (e.g., NIELSEN 1955a, SPRINGETT 1963, NURMINEN 1967). However, the low winter temperature apparently affected the vertical distribution of *C. sphagnetorum*. The worms were more deeply distributed in January and February. The deep distribution that occurred in June 1974 was probably caused by drought.

Changes in vertical distribution have been attributed to active movement by the worms (e.g. SPRINGETT et al. 1970) and/or to differential mortality rate (e.g. NURMINEN 1967). An active vertical movement seems plausible also for the Jädraås conditions during the winter since the absolute numbers of *C. sphagnetorum* remained unchanged and growth would have been at a low level. For June 1974 none of the possible explanations above could be ruled out since the population density had decreased.

5.3. Abundance and biomass

The seasonal variations in abundance of *C. sphagnetorum* suggest a population cycle with two yearly peaks of about equal magnitude, one occurring in late autumn-winter and one in summer. Previous findings concerning *C. sphagnetorum* in Fennoscandian forests also indicated high population densities twice a year. NURMINEN (1967) found early summer and autumn peaks and winter minima in his three-year study in Finland. The investigation by ABRAHAMSEN (1972) in Norway did not cover the winter period, but his population data showed a peak in July after which the population first declined and then increased again in October, when the study was finished.

In contrast, investigations in Denmark (NIELSEN 1955b), Great Britain (O'CONNOR 1957, PEACHEY 1963, STANDEN 1973) and Norway at a high altitude (KLUNGLAND 1979) indicated population peaks only once a year namely in late summer or autumn. The reason for this difference is probably to be found in different soil moisture and temperature conditions (O'CONNOR 1957, NURMINEN 1967). O'CONNOR suggested that in temperate oceanic regions like Britain moisture conditions were almost always favourable and that the yearly peak was due to optimal temperature in summer and autumn. In Denmark, on the other hand, moisture would be limiting in summer and the yearly peak occurred in autumn. NURMINEN (1967) proposed that in more northerly continental regions, like Finland, temperature was limiting in winter and moisture in summer. Consequently, population peaks occurred in spring and autumn.

The situation at Jädraås did not fully agree with any of the patterns described above. The summer peaks followed increased soil moisture conditions (cf. Fig. 1) after dry periods. However, the decrease in abundance in September occurred despite the fact that soil moisture was still at a high level. This could possibly be related to increased mortality during the fragmentation period.

The duration of the winter maximum was probably determined by soil temperature, such that the decline started when soil temperature fell below zero for a longer period. At Jädraås this occurred from February to March. Although different enchytraeid species appear to be more or less well adapted to cold conditions (DOZSA-FARKAS 1973) temperatures of −3 °C and lower have been found to reduce densities drastically in field situations (HUHTA 1978).

The seasonal variations in abundance and those in biomass of *C. sphagnetorum* at the Jädraås site accompanied one another in time. There was, however, one important difference. The summer peaks of the biomass were only half as high as the winter peak. This is clearly due to the summer maxima consisting of small worms. From the size distribution data it is also evident that the summer maxima were preceded by periods of fragmentation. In 1974 the summer maximum occurred one month prior to the period of smallest mean worm size, whereas that of 1975 coincided with this period. In both summers the worms fragmented most frequently during a fairly dry period and the individual worm size started to increase when the soil moisture increased.

The winter maximum in abundance of *C. sphagnetorum* was of a different character as it occurred when the individual worm size had reached its highest value and hence the population also had its maximum biomass. This population- and worm growth took place during the autumn and early winter when soil moisture was consistently high.

Soil temperature in the humus layer did not fall below zero until December. In the mineral soil it remained above zero until February. In January and February most of the population of *C. sphagnetorum* was present in the mineral soil.

Thus it seems that the population size and the dominance of *C. sphagnetorum* over other species are dependent on occasional droughts, while growth of the individual worm is favoured by moist soil conditions. Whether this is valid for *C. sphagnetorum* in general is not clear since most of the previous studies on *C. sphagnetorum* as well as on enchytraeids on the whole have dealt with abundance only and considerations about seasonal variations are often described on the basis of rather few sampling occasions. One exception is the study by Standen (1973), who found late summer abundance peaks in two consecutive years in a blanket bog site. Standen reported that fragments of worms were found all through the year, bur that the rate of fragmentation was highest in May—June in both years. In studies in the same area as Standen, Peachey (1963) also reported high abundances in late summer or early autumn. He considered the higher abundance in autumn to be due to addition of small worms as he found that enchytraeid biomass decreased at that time. Previous studies on enchytraeids in coniferous forests in Scandinavia have not reported both abundance and biomass figures for longer periods. Huhta & Koskenniemi (1975) covered the period from May to October. Their figures give a weak indication of a fragmentation period in August when a fairly high abundance corresponded to a moderate biomass. In September both abundance and biomass had maxima. Abrahamsen (1972, 1973) reported abundance and biomass figures for enchytraeids in a Vaccinio-Pinetum locality where the abundance figures for *C. sphagnetorum* and for total enchytraeids were almost identical over the whole investigation period. However, his two papers indicate that the abundance maximum of *C. sphagnetorum* in July coincided with low enchytraeid biomass and that about twice as high enchytraeid biomass occurred in the autumn when the abundance was about 60 % of the maximum. This would suggest that also in this Norwegian site *C. sphagnetorum* fragmented in early summer. There is no reason to believe that soil moisture itself is the only factor causing the high population densities found in autumn and summer. Undoubtedly, the enchytraeids also need a sufficient supply of food. The feeding preferences of *C. sphagnetorum* are not known in detail. Gut contents of the worms normally consists of a mixture of litter remains and microorganisms (e.g. Latter & Howson 1978).

C. sphagnetorum has been found to be more abundant in microhabitats with *Calluna* and *Eriophorum* than in those with *Sphagnum* (Standen & Latter 1977). Consistent with this, Latter & Howson (1978) showed in laboratory experiments that natural *Calluna* and *Eriophorum* litter was preferred to *Sphagnum* litter. Irradiated litter was suitable food only after treatment with enzymes. Feeding experiments with *C. sphagnetorum* on pure fungal substrates gave poor or no growth of the worms (Springett & Latter 1977). Apparently the combination of litter and microorganisms was essential for *C. sphagnetorum*, as was also suggested by Springett (1964). Decomposition experiments at the Jädraås site (Berg et al. 1980) also indicated that *C. sphagnetorum* feeds on litter and microorganisms as both weight loss and chemical composition of the litter substrate were found to be affected by the presence of enchytraeids.

The food selection experiments referred to above suffer from the limitation that they did not include any root litter as a tested food item. At the Jädraås site, root litter might be an important food source for *C. sphagnetorum* since annual below-ground litter production (Persson 1980a) is in the same order of magnitude (c. 240 g dw m^{-2} yr^{-2}) as in the above-ground litter production (Flower-Ellis & Olsson 1978). At an adjacent site with a young pine forest, Persson (1980b) found an increase in the FH-layer of the fine root necromass of pine in early July and in August—September 1974, i.e., during the relatively dry periods preceding the biomass peaks of *C. sphagnetorum* that year. In the studies of active fungal biomass for three consecutive years at the present Jädraås site, Söderström (1979) found population peaks twice a year, in the early summer and in the autumn, in connection with high moisture contents. For bacteria at the same site, Clarholm & Rosswall (1980) found population fluctuations to be strongly moisture dependent. Thus, there is a fairly clear covariation between fungal and bacterial increments and decomposition on one hand and the biomass increase of *C. sphagnetorum* on the other.

To summarize, it seems reasonable to assume the following pattern for the population development of *C. sphagnetorum.* The worms fragment throughout the year, but the rate increases in dry periods during which food availability is poor but is gradually building up through root death and accumulation of above-ground litter caused by low microbial activity. In subsequent wet periods the worm biomass increases due to the improved food availability resulting from enhanced microorganisms activity and decomposition.

5.4. Respiration

The respiration equation used was that proposed by PERSSON & LOHM (1977) for enchytraeids in general. There are also expressions available for *C. sphagnetorum*, namely the equations for active and passive worms, respectively, derived by STANDEN (1973). Despite this, the former equation was used for the following reasons. STANDEN's respiration curves do not cover the range of worm sizes needed for the present data while that of PERSSON & LOHM does. For computerizing it was easier to handle the single equation given by PERSSON & LOHM than the separate estimates for active and passive rates, as well as head and tail fragments given by STANDEN.

The weight specific oxygen consumption rate of *C. sphagnetorum* calculated according to PERSSON & LOHM yielded a curve that is intermediate to STANDEN's curves for active and passive worms in the weight interval that is covered by both these authors. For small worms (50—200 μg live weight) the former curve approaches the respiration rate values given by STANDEN for worm fragments.

The carbon flow through the soil organisms at the Jädraås site and the share of the enchytraeids have been discussed previously (PERSSON et al. 1980). Because of the use of rougher estimates, due to the assumption of an average individual worm biomass, the previous presentation contained slight overestimates (10—20 %) of the enchytraeid respiratory metabolism in the period July—September 1974, while the respiratory metabolism was somewhat underestimated (about 23 %) during the rest of the period from May 1974 to June 1975. However, the more detailed population data now gathered do not influence the crucial parts of the discussion in PERSSON et al. (1980) where one of the conclusions was that a great part of the annual production of the microorganisms is consumed by the animals. Further, it was suggested that predation was probably important for reduction of the microbial biomass in the upper soil layer. On a yearly basis *C. sphagnetorum* contributed, on average, 20—25 % to total soil animal biomass and respiration. Hence, as *C. sphagnetorum* most probably could be classified as a litter/microorganism feeder (cf. above), its contribution to the release of bioelements from the microbial population is probably significant.

5.5. Nitrogen content

The four-month period of decrease in population biomass during February—June implies a noticeable input of nitrogen to the soil at the beginning of the growing season, at a time when it is in strong demand by plants. An estimated 76 mg m^{-2} nitrogen input from dead worms during four months could be compared with the total root uptake down to 20 cm in the mineral soil of an estimated 3,300 mg m^{-2} yr^{-1} at the present site (BRINGMARK 1977), of which 73 % was taken from the FH-layer (STAAF & BERG 1977). The reverse phenomenon, namely the retention of nitrogen in worm biomass, took place during a period when competition for nitrogen from the plants would have decreased as the growing period had ended.

6. Conclusions

(1) The almost complete dominance of *C. sphagnetorum* over other enchytraeid species at Jädraås seems to be due to its asexual reproduction through fragmentation. This is a reproductive strategy that would be advantageous in recovering after the dry periods that occur with fairly high regularity at the site.

(2) The fragmentation rate of *C. sphagnetorum* increased during dry periods in the summers when the abundance peaked, while the individual growth rate was highest during wet periods. Maxima of abundance as well as biomass were reached in the winter.

(3) The growth of individual *C. sphagnetorum* mainly occurred in wet periods when high microorganism activity and decomposition of both root litter and above-ground litter provided increased food for the worms.

(4) The predation by *C. sphagnetorum* on the microbial population presumably was of significance for the release of nutrients bound in microorganisms.

(5) The release of nitrogen bound in worms was highest in the berginning of the vegetation period whereas nitrogen was immobilizied through the building up of worm biomass, especially during autumn.

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Address of the author: Dr. Heléne Lundkvist, Zoologiska Institutionen, Uppsala Universitet [Department of Zoology, University of Uppsala] Box 561, S - 751 22 Uppsala, Sverige [Sweden].

Significant differences ($p < 0.05$) between the monthly samplings May 1974 to September 1975 in the investigated characteristics of the *Cognettia sphagnetorum* population at Jädraås. The soil horizons are denoted: 1 = A_{00}—A_{02}, 2 = A_2, 3 = B and 4 = total soil core. It should be noted that i) possible incidental significances due to multiple comparisons and ii) the variance in respiration data taken from the literature are not accounted for in the analyses of variance.

Matrix 1,
Abundance, *cf.* Fig. 2.

	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A
	1974								1975							
1974																
J	-- --															
J	-- --	1- -4														
A	-- --	-- --	-- --													
S	-- --	1- --	-- --	-- --												
O	-- --	1- --	-- --	-- --	-- --											
N	-- --	1- --	-- --	-- --	-- --	-- --										
D	-- --	-- -4	-- --	-- --	-2 --	-- --	-2 --									
1975																
J	-- 3-	-- 3-	1- 3-	-- 3-	-2 3-	-- 3-	-2 3-	-- 3-								
F	-- 3-	-2 -4	-2 --	-2 3-	-2 3-	-2 3-	-2 --	-- --	-- --							
A	-- --	-- --	1- -4	-- --	-- --	-- --	1- --	-- -4	-2 3-	-2 -4						
M	-- --	-- --	1- -4	-- --	-- --	-- --	-- --	-- --	-- 3-	-2 34		-- --				
J	-- --	-- --	1- -4	-- --	1- --	1- -4	1- -4	-2 -4	-2 34	-2 34		-- --	-- --			
J	-- --	-- --	1- --	-- --	-- --	-- --	-- --	-- --	-- 3-	-2 34		-- --	-- --	-- --		
A	1- --	1- -4	-- --	1- --	1- --	1- --	-- --	12 --	12 3-	12 3-		1- -4	1- -4	1- -4	1- -4	
S	-- --	1- --	-- --	-- --	-- --	-- --	-- --	-2 --	-2 3-	-2 3-		1- --	-- --	1- --	-- --	-- --

Matrix 2,

Size (No. of segments), *cf.* Fig. 4.

	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A
1974 J	1- --															
J	1- -4	-- --														
A	1- 34	-- -4	1- -4													
S	12 34	-2 34	-- --	-- --												
O	-- --	1- -4	1- -4	1- -4	12 34											
N	-- --	12 --	-2 -4	12 34	12 34	-- --										
D	-2 -4	12 -4	12 -4	12 34	12 34	-2 -4	-- -4									
1975 J	-2 -4	12 -4	12 -4	12 34	12 34	-2 -4	1- -4	-- --								
F	12 -4	12 -4	12 34	12 34	12 34	12 -4	1- -4	1- -4	-- --							
A	-- -4	12 -4	12 34	12 34	12 34	1- -4	1- -4	-- --	-- --	-- --						
M	-- --	12 -4	12 34	12 34	12 34	-- --	-- --	-- --	-- -4	1- -4		1- --				
J	-- --	-- --	-- --	1- 34	-2 34	-- --	-- --	-2 -4	12 -4	12 -4		1- -4	-- -4			
J	12 -4	1- -4	1- -4	-- --	1- 3-	12 -4	12 -4	12 -4	12 -4	12 -4		12 -4	12 -4	12 -4		
A	12 3-	-- 34	-- --	-- --	-- --	1- -4	12 34	12 34	12 34	12 34		12 34	12 34	-2 34	1- --	
S	-2 -4	12 -4	12 34	12 34	12 34	-2 --	-- --	-- --	-- -4	1- -4		1- -4	-- --	-2 --	12 -4	12 34

1974 1975

Matrix 3,
Individual dry weight, *cf.* Fig. 6.

	M 1974	J	J	A	S	O	N	D	J 1975	F	M	A	M	J	J	A
1974 J	1- --															
J	1- -4	-- --														
A	1- 34	-- -4	-- --													
S	12 34	-- 34	-- --	-- --												
O	-- --	1- -4	1- -4	1- -4	12 34											
N	-- --	12 -4	-2 -4	12 34	12 34	-- --										
D	-2 -4	12 -4	12 -4	12 34	12 34	-2 -4	-- -4									
1975 J	-2 -4	12 -4	12 -4	12 34	12 34	-2 -4	1- -4	-- --								
F	12 -4	12 -4	12 34	12 34	12 34	12 34	1- -4	1- -4	-- --							
A	1- -4	1- -4	12 34	12 34	12 34	1- -4	1- -4	-- --	-- --	-- --						
M	-- --	12 -4	12 34	12 34	12 34	-2 --	-- --	-- --	-- -4	1- -4		1- --				
J	-- --	1- --	-- 4	1- 34	12 34	-- --	-- --	-2 -4	12 -4	12 -4		1- -4	-- --			
J	12 -4	-- -4	1- -4	-- --	1- 3-	12 -4	12 -4	12 -4	12 -4	12 -4		12 -4	12 -4	12 -4		
A	1- 34	-- -4	-- --	-- --	-- --	1- -4	12 34	12 34	12 34	12 34		12 34	12 34	12 34	1- --	
S	-- --	12 -4	12 34	12 34	12 34	-2 --	-- --	-- -4	-- -4	1- -4		1- -4	-- --	-- --	12 -4	12 34

Matrix 4,
Population dry weight, *cf.* Fig. 7.

	M 1974	J	J	A	S	O	N	D	J 1975	F	M	A	M	J	J	A	S
1974 J	-- --																
J	-- --	1- --															
A	-- --	-- --	-- --														
S	-- --	-- --	-- --	-- --													
O	-- --	1- --	-- --	-- --	-- --												
N	-- --	1- --	-- --	-- --	-- --	-- --											
D	-- --	-2 -4	-2 --	-2 -4	-2 34	-- --	-2 --										
1975 J	-- 3-	-2 34	-2 3-	-2 34	-2 34	-2 3-	-2 3-	-- 3-									
F	-2 34	12 -4	-2 -4	-2 34	-2 34	-2 34	-2 -4	-- --	-- --								
A	-- --	-- --	-- --	-- --	-- --	-- --	1- --	-2 -4	-2 3-	-2 -4							
M	-- --	-- --	-- --	-- --	-- --	-- --	-- --	-2 -4	-2 3-	-2 34		-- --					
J	-- --	-- --	1- --	-- --	-- --	1- --	1- -4	-2 -4	-2 34	12 34		-- --	-- --				
J	-- --	-- --	1- --	-- --	-- --	1- --	1- --	-2 -4	-2 34	12 34		-- --	-- --	-- --			
A	-2 --	1- --	-- --	-- --	-- --	-- --	-- --	-2 3-	-2 3-	-2 34		1- --	-- --	1- --	1- --		
S	-- --	-- --	-- --	-- --	-- --	-- --	-- --	-2 --	-2 3-	-2 34		-- --	-- --	-- --	-- --	-- --	

Matrix 5,
Individual respiration, *cf*. Fig. 8.

1974 J	-2 -4															
J	-2 -4	-- --														
A	-2 --	-- 34	1- -4													
S	-- 34	-2 34	12 34	-2 34												
O	12 34	12 34	12 34	12 34	1- -4											
N	12 34	12 34	12 34	12 34	12 -4	1- -4										
D	12 34	12 34	12 34	12 34	12 -4	1- -4	-- --									
1975 J	12 34	12 34	12 34	12 34	12 -4	12 34	-- --	-- --								
F	12 34	12 34	12 34	12 34	12 -4	12 34	-- --	-- --	-- --							
D	12 34	12 34	12 34	12 34	12 -4	12 34	-- --	-- --	-- --	-- --						
M	-- --	-2 34	12 -4	-2 --	-- 3-	12 -4	12 34	12 34	12 34	12 34		12 34				
J	12 -4	-- --	-- --	1- 34	12 34	12 34	12 34	12 34	12 34	12 34		12 34	12 34			
J	-2 3-	-- 34	1- 34	-- 3-	-2 34	12 34	12 34	12 34	12 34	12 34		12 34	-2 34	1- 34		
A	-2 --	-- 34	-- --	1- --	12 34	12 34	12 34	12 34	12 34	12 34		12 34	12 -4	-- 3-	1- 3-	
S	-2 --	-- -4	-- --	-- --	-2 34	12 34	12 34	12 34	12 34	12 34		12 34	-2 34	-- -4	-- 3-	-- --
	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A
	1974								1975							

Matrix 6,
Population respiration, *Cf*. Fig. 9.

1974																
J	-- 3-															
J	1- 3-	1- -4														
A	-- --	-- 3-	1- -4													
S	-2 --	-2 3-	12 34	-- --												
O	-- --	-- 3-	1- 34	-- --	-- --											
N	-2 --	-2 --	12 -4	-- --	-- --	-- --										
D	-- --	-- --	1- -4	-- --	-- --	-- --	-- --									
1975																
J	-- 3-	-- --	1- -4	-- --	-- 3-	-- 3-	-- --	-- --								
F	-- --	-- --	1- -4	-- --	-- --	-- --	-- --	-- --	-- --							
A	-2 -4	-2 3-	12 34	1- -4	-- --	-- --	-- --	-- --	-- 3-	-- --						
M	-- --	-- 3-	1- 34	-- --	-- --	-- --	-- --	-- --	-- 3-	-- --		-- --				
J	-- --	-- 3-	1- 34	-- --	-- --	-- --	-- --	-- --	-- 3-	-- --		-- --	-- --			
J	-- --	-- 3-	1- 34	-- --	-- --	-- --	-- --	-- --	-- 3-	-- --		-2 --	-- --	-- --		
A	12 --	12 34	-2 34	1- -4	1- -4	1- -4	1- -4	1- -4	1- 34	1- -4		1- -4	1- -4	1- -4	1- -4	
S	-2 --	-- 3-	12 34	-- --	-- --	-- --	-- --	-- --	-- 3-	-- --		-- -4	-- --	-- --	-- --	1- -4
	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A
	1974								1975							

Synopsis: *Original scientific paper*

LUNDKVIST, H., 1982.
Population dynamics of *Cognettia sphagnetorum* (Enchytraeidae) in a Scots pine forest soil in Central Sweden.
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The population dynamics of *Cognettia sphagnetorum* (VEJD.) in a mature Scots pine stand was studied through monthly samplings May 1974 to September 1975. Asexual (fragmenting) worms only were found. The individual worms were classified to size according to their number of segments. Fresh weight and dry weight of individual worms were determined. Respiration was calculated from literature data. The nitrogen content of *C. sphagnetorum* was 10.8 % of the dry weight.

The abundance of *C. sphagnetorum* peaked (23,000 ind. m^{-2}) in late summer and in winter. Minimum abundance (6,000 ind. m^{-2}) occurred in early summer. Maximum biomass (6.5 g m^{-2} fresh weight) occurred in winter. The fragmentation rate of the worms increased during dry periods in the summer and the growth rate was highest when soil moisture was consistently high in the autumn and when food availability improved. The population density declined in late winter at a time when soil temperature fell below ± 0 °C for a longer time. 76 mg N m^{-2} was estimated to have been released to the system as a result of the population decline in February to June. Over the year an estimated 2,200 mg C m^{-2} was respired by the *C. sphagnetorum* population, i.e., on average 20—25 % of total soil animal respiration at the site. Possible selective advantages of asexual reproduction in *C. sphagnetorum* are discussed.

Key words: **Abundance, asexual reproduction, biomass, fragmentation, nitrogen content, podzol, respiration, seasonal dynamic, vertical distribution.**